INFLUENCE OF *AMMOPHILA ARENARIA* ON FOREDUNE PLANT MICRODISTRIBUTIONS AT POINT REYES NATIONAL SEASHORE, CALIFORNIA

ROBERT S. BOYD
Department of Botany and Microbiology,
Alabama Agricultural Experiment Station,
Auburn University, AL 36849-5407

ABSTRACT

Association analysis was used to explore the microdistributions of foredune species. The introduced beachgrass, *Ammophila arenaria,* affected the microdistributions of some species. *Poa douglasii, Cakile maritima,* and *Abronia latifolia* were positively associated with *Elymus mollis.* These four were negatively associated with *Ammophila,* whereas *Mesembryanthemum chilense, Ambrosia chamissonis,* and *Camissonia cheiranthifolia* were not influenced by *Ammophila.* Positive associations between *Cakile/Agoseris apargioides* and *Mesembryanthemum/Ambrosia* were also detected. Examination of microdistributions relative to *Ammophila* patch borders indicated that only *Cakile* was significantly influenced by distant-dependent rodent foraging from *Ammophila* patches.

Marine beach communities have long attracted ecologists because of the pronounced zonation of plant species along the land/sea gradient. Many studies have examined the importance of physical factors (e.g., salt spray) which are primarily responsible for this zonation (Barbour 1978; Barbour and DeJong 1977; Doing 1985; Fink and Zedler 1990; Oosting 1945). Fewer attempts have been made to examine the microdistributional occurrences of beach plant species caused by other interactions which are not directly related to this gradient of physical factors (e.g., predation, allelopathy, or competition).

West Coast beach foredune vegetation from Canada through Central California is dominated by *Ammophila,* brought from Europe in the late 1800's to stabilize active sand dunes. It has replaced a native grass species (*Elymus mollis*) as the dominant member of the foredune community throughout the range of *Elymus.* A number of studies have pointed out some of the differences between the communities formed by these two grasses: *Ammophila* communities have fewer species of plants (Breckon and Barbour 1974) and burrowing insects (Slobodchikoff and Doyen 1977), a taller and more dense leaf canopy (Pavlik 1982), and the foredune itself is usually taller than in *Elymus* communities (Cooper 1967). The observed decrease in species richness of *Ammophila*-dominated areas has not

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been explained. It is intuitively obvious that the greater density of *Ammophila* culms and their taller canopy usurp aboveground space and therefore crowd out other species. Furthermore, the superior sand-stilling qualities of *Ammophila* may decrease the ability of other species to disperse (via the wind) into *Ammophila* areas. This latter factor may be partially offset by the protection from salt spray and sand-blast provided by a stand of *Ammophila,* as suggested by Breckon and Barbour (1974).

Herbivores also can have important effects on vegetation patterns. In cases where their activity varies spatially, as when foraging outward from a refuge from predation, they can cause zonation patterns by creating an herbivory gradient (Bartholemew 1970; Huntly 1987; Rood 1970). Pitts and Barbour (1979) showed that activities of the deer mouse, *Peromyscus maniculatus,* were concentrated in areas densely covered by *Ammophila.* They also showed that the rodents were omnivorous, consuming seeds and herbage of a number of plant species along with insects. Their observations suggest that higher levels of herbivore activity may be another factor which acts to decrease plant species richness in areas dominated by marram grass. In a recent paper, I showed that the microdistribution of *Cakile maritima* was strongly influenced by predation of seedlings and fruits (Boyd 1988). Because foraging by the main predator (*Peromyscus maniculatus*) was closely correlated with areas of high plant cover, borders of dense clumps of *Ammophila* had fewer *Cakile* plants. These results suggested that rodent predation might be a factor that contributes to decreasing species richness of plants and arthropods in areas dominated by *Ammophila.*

In this paper, data gathered during an earlier investigation of *Cakile* (Boyd 1988) were used to compare pairwise associations between foredune taxa, including the influence of *Ammophila* on these associations. Microdistributions of these taxa relative to *Ammophila* patches also were used as an indirect test of the significance of rodent herbivory in determining species richness in *Ammophila*-dominated areas.

METHODS

Study site. Point Reyes is located on the California coast 50 km north of San Francisco. The northern beach of Point Reyes National Seashore forms one of the longest unbroken stretches of beach in northern California, extending 18 km along the coast. As with most northern West Coast beaches (Barbour et al. 1976), the foredune is mostly dominated by *Ammophila arenaria.* One exception is a 1-km section of Kehoe Beach, where *Ammophila* patches are found interspersed with patches of the native grass, *Elymus mollis.* The *Ely-*

mus areas contain plant species which are relatively scarce in the *Ammophila* areas.

Microdistribution pattern. To document species microdistributions relative to the *Ammophila* patches, I selected a 0.5-km section of foredune which had both *Ammophila*-dominated and *Elymus*-dominated areas. *Ammophila* patches selected for sampling within this area were chosen so that transects would parallel the tideline. In this way, differences in abundance due to differences in species zonation would be avoided. At each of seven *Ammophila* patches, six contiguous 17 m-long transects were established running outward from patch borders into surrounding *Elymus* areas. For each transect, a 1-m^2 border plot was subjectively chosen. I chose border plots by determining where the amount of bare space approached that of non-*Ammophila* areas. Although the six transects at each *Ammophila* patch were contiguous, border plots may not have been contiguous, depending on the distribution of *Ammophila* within each transect.

Once the border plot was chosen, a 1-m^2 sampling frame was placed over the plot and the cover of each plant species present was recorded. Cover values were estimated for living plant parts only, except for the beachgrasses, where dead parts often formed a large fraction of the total cover. The area of bare sand present was calculated by subtracting total plant cover from 100%, except in rare cases where plant cover was high and significant canopy overlap occurred. In those cases, bare sand area was estimated directly in the field. From the border plot, two 1-m^2 plots were located farther into the *Ammophila* patch, and 14 1-m^2 plots were placed out into the surrounding *Elymus* area (Fig. 1). Altogether these formed a

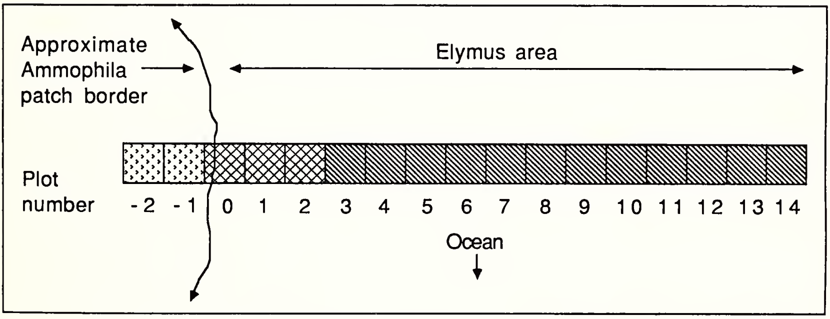

FIG. 1. Example sampling transect of 17 contiguous 1–m^2 plots established parallel to the beachfront. This transect is divided into within-*Ammophila* patch plots (plot numbers −2 and −1), border plots in the *Elymus* area (plot numbers 0–2), and more distant *Elymus* area plots (3–14). Not shown are the other five contiguous transects placed in each sampled area.

17-m long transect beginning 2 m inside an *Ammophila* patch. Sampling was done in November 1984, at the end of the reproductive season for *Cakile.*

The influence of herbivore activity on plant distribution was assessed indirectly by analyzing plant distribution patterns. If a species were negatively affected by amensalism with *Ammophila,* it would be scarce within the *Ammophila* patch, but its abundance in the border area should be similar to that farther outside the patch. As shown by Boyd (1988), a species affected by rodent herbivory would have decreased abundance beyond the patch border into quadrats 0–2 (Fig. 1). I compared the frequency of each species in the first 5 m (quadrats −2 to 3) with that in quadrats 4 to 14. I then compared frequency in the border 3 m (plots 0, 1, and 2) versus the remaining 12 m (plots 3–14) by the chi-square test (Zar 1984). Because of the relatively small numbers of quadrats used, I used the 0.01 probability level for this and the association analysis to decrease the chance of falsely concluding that pattern existed (Zar 1984). Species with overall frequency less than 5% were excluded from both analyses.

Association analysis. Association analysis between taxa may give clues to the existence of underlying ecological relationships (Mueller-Dombois and Ellenberg 1974). All pairs of species were examined for significant associations. The influence of *Ammophila* on these associations was assessed by testing for association on all data, and then excluding those quadrats containing *Ammophila* and testing for association again.

RESULTS

A total of 12 species was found along the transects (Table 1). Nine species were relatively abundant, being present in more than 5 percent of the quadrats. Three species (*Ammophila arenaria, Cakile maritima* and *Mesembryanthemum chilense*) were non-native. *Cakile* was the most short-lived species present, since most individuals do not survive more than two growing seasons (Boyd 1986). Those species with more than 5 percent frequency are, with the exception of *Agoseris apargioides,* widespread taxa characteristic of California beaches (Breckon and Barbour 1974).

Microdistribution pattern. Only 4 species showed significant microdistribution patterns relative to *Ammophila* patches (Table 2). Decreased frequency of *Ammophila* was not surprising because of the way patch boundaries and transects were delineated. This decrease was not influenced by inclusion of border plots (quadrats 0–2) in the analysis. The other two grasses in the study area (*Elymus* and *Poa*) were negatively affected by *Ammophila.* Both had significantly lower abundances within *Ammophila* patches but not in bor-

TABLE 1. FREQUENCY OF OCCURRENCE OF PLANT TAXA IN ALL SEVEN SAMPLING AREAS. Frequency is expressed as percentage of the 1-m^2 quadrats (n = 714) in which each species was present.

Species	Frequency
Elymus mollis Trin. ex Spreng.	87.1
Ammophila arenaria (L.) Link.	23.9
Cakile maritima Scop.	22.8
Mesembryanthemum chilense Mol.	20.0
Abronia latifolia Eschs.	16.9
Agoseris apargioides ssp. *maritima* (Sheld.) Q. Jones	8.7
Poa douglasii Nees.	8.1
Camissonia cheiranthifolia (Hornem. ex Spreng.) Raimann in Eng. & Prantl ssp. *cheiranthifolia*	7.7
Ambrosia chamissonis (Less.) Greene	7.6
Atriplex leucophylla (Moq.) D. Dietr.	2.1
Erigeron glaucus Ker.	0.7
Gnaphalium sp.	0.4

der areas, indicating that *Ammophila*'s negative influence did not extend beyond patch borders. *Cakile* showed a third pattern, decreasing in frequency both inside and in a zone bordering the *Ammophila* patches.

Association analysis. Several species (*Mesembryanthemum, Ambrosia,* and *Agoseris*) were not influenced by *Ammophila. Ammophila* had a large influence on other species associations, influencing them both directly and indirectly. *Elymus, Poa, Abronia,* and *Cakile* were all negatively associated with *Ammophila* (Table 3), indicating decreased frequency inside *Ammophila* patches. Positive associations between *Elymus* and *Cakile, Ambrosia,* and *Poa* were the indirect result of their negative associations with *Ammophila.* This was demonstrated by lack of significant associations when *Ammophila*-containing quadrats were excluded. Two other associations involving *Elymus* (with *Mesembryanthemum* and *Ambrosia*) seemed

TABLE 2. CHANGE IN FREQUENCY OF FOREDUNE SPECIES AS AFFECTED BY THE *AMMOPHILA* PATCH BORDER. Only those species for which a significant result ($P < 0.01$) was obtained are included. ns = not significant.

	Quadrats compared	
Species	−2 to +2 versus +3 to +14	0 to +2 versus +3 to +14
Ammophila arenaria	Decrease	Decrease
Elymus mollis	Increase	ns
Poa douglasii	Increase	ns
Cakile maritima	Increase	Increase

TABLE 3. STATISTICALLY SIGNIFICANT PAIR-WISE ASSOCIATIONS (POSITIVE OR NEGATIVE) BETWEEN SPECIES IN THE SAMPLED QUADRATS. Tests for association were made both for all quadrats and for those quadrats in which *Ammophila* was absent. Only those species pairs which showed a significant association in at least one case are listed. ns = no significant association (at $P < 0.01$).

Species pair	All quadrats	*Ammophila* quadrats excluded
Ammophila/Elymus	Negative	—
Ammophila/Poa	Negative	—
Ammophila/Cakile	Negative	—
Ammophila/Abronia	Negative	—
Elymus/Cakile	Positive	ns
Elymus/Abronia	Positive	ns
Elymus/Poa	Positive	ns
Elymus/Mesembryanthemum	ns	Positive
Elymus/Ambrosia	ns	Negative
Cakile/Agoseris	Positive	Positive
Mesembryanthemum/Ambrosia	Positive	Positive

to be influenced by *Ammophila,* being significant only when *Ammophila* quadrats were excluded from the analysis. These reflected an interaction between these species, one resulting in a positive and the other a negative association.

Only two interactions were detected which were not influenced by *Ammophila. Cakile* and *Agoseris* were positively associated and *Mesembryanthemum* and *Ambrosia* also were positively associated. I obtained this result both when *Ammophila*-containing plots were included in or excluded from the analysis.

DISCUSSION

Reports of lowered species richness of *Ammophila*-dominated beaches do not indicate which species may be most sensitive to *Ammophila.* Barbour et al. (1976) surveyed 34 Pacific Coast beaches from California to Washington. Half were classified as *Ammophila*-dominated and half as dominated by *Elymus, Cakile,* or other species. For comparative purposes I have summarized species presence on these beaches (% of beaches surveyed, presence on *Ammophila*-dominated vs. non-*Ammophila*-dominated beaches) as follows: *Ambrosia* (35 vs. 71), *Camissonia* (0 vs. 24), *Abronia* (59 vs. 82), *Poa* (18 vs. 6), *Cakile* (71 vs. 100). Based on this information, we might conclude that *Ambrosia, Camissonia, Abronia* and *Cakile* were all sensitive to the presence of *Ammophila* because they were found less frequently on *Ammophila*-dominated sites. The results of my study showed *Cakile, Abronia,* and *Poa* to be negatively associated with *Ammophila,* but *Camissonia* and *Ambrosia* were not affected by *Ammophila.* These contrasting results may be due in part to the confounding factor of non-overlapping species geographic distributions for some of these taxa (Breckon and Barbour 1974). The small scale at which I have examined associations also undoubtedly is a factor as it allows detection of fine-grained patterns.

Few other small scale examinations of Pacific Coast beach vegetation have been made. Bluestone (1981) reported no consistent patterns of association among species on the beach and foredune of Salinas River State Beach, California, but at that time little *Ammophila* was present on that site. Pitts (1976) reported a strong positive association of *Ambrosia* and *Cakile* in a large foredune quadrat at Point Reyes. I found these species to lack significant association in my study area.

The differential response of species to *Ammophila* may be due to a number of factors. Average cover inside an *Ammophila* patch was high, 50% for quadrat −2 (Boyd 1988). *Ammophila* and *Elymus* were by far the tallest of the species encountered. Therefore they would have shaded the other species encountered, but this shading effect may be positive or negative depending on the ecological circumstances. Payne (1980) reported that *Cakile edentula* plants growing under *Ammophila breviligulata* on Great Lakes beaches were often larger than unshaded plants when water was not limiting. She attributed this effect to *Ammophila* acting as a shelter for *Cakile* but pointed out that if water became limiting these sheltered plants usually died (presumably from competition with *Ammophila* for water). Barbour et al. (1976) mentioned a potential positive windscreen effect of *Ammophila* shoots, but this may be countered by greater sand accumulation in *Ammophila* areas (Barbour et al. 1985).

These results imply that the spread of *Ammophila* has been accompanied by decreases in abundance of some native species (*Elymus, Poa, Cakile,* and *Abronia*). I know of no historical data to verify this implication, but if true it may provide a partial explanation for decreased species diversity of arthropods in *Ammophila* areas (Slobodchikoff and Doyen 1977) as changes in the abundance of the plant species may have eliminated some dependent arthropod species. Another factor may be higher predation of insects by *Peromyscus* in *Ammophila* areas, as Pitts and Barbour (1979) demonstrated that they consume insects in addition to plant material.

The beach area studied has had both *Elymus* and *Ammophila* present for a long time (Cooper 1967), and they may have reached an equilibrium. If so, then the patterns observed in this study are not due to recent invasion by *Ammophila* but reflect the sorting of species across *Ammophila* patch borders over time. However, beach and dune systems are characterized by a rapidly changing habitat and differential patterns of colonization may be included in these results (Williams and Williams 1984).

Cakile was the only species for which evidence of a rodent-foraging effect was detected. The failure of other species to show distance effects similar to those of *Cakile* does not mean mice have no effect on them. It does imply that mice do not play as important a role in the microdistribution of these species as with *Cakile.* Their influence on *Cakile* may be greater because it is an annual or biennial (Maun et al. 1990) and hence more sensitive to seed and seedling predation. The other taxa are perennials and some reproduce asexually. Experiments conducted by Pitts and Barbour (1979) indicate *Cakile* may be a more important food source compared to the other species. They found *Cakile* leaves and fruits were preferred by *Peromyscus.* Fruits of *Poa* and *Ammophila* also were taken readily. The only other species encountered in my study and included in their tests was *Abronia,* which was not eaten. Rodent consumption of *Cakile* seeds has been noted on other California beaches (Johnson 1963), but not on Great Lakes (Payne and Maun 1984) or Atlantic Coast beaches (Keddy 1982), in spite of the ubiquitous distribution of *Peromyscus.* Rodent activity may be an important ecological factor for some beach plants only on the Pacific Coast, but it may simply have been overlooked in other studies.

The lack of a rodent-foraging effect for species other than *Cakile* implies that rodent herbivory is not a major factor in determining species microdistributions near *Ammophila* on the beach and foredune. In general, *Ammophila* is not an important food source for many herbivores. Huiskes (1979) noted that vegetative parts are disliked by rabbits, sheep, and cattle, and that *Ammophila* supports no monophagous insects. Pavlik (1982) noted that *Ammophila* was less desirable to herbivores than *Elymus.* Although it is tempting to suggest an herbivore-mediated mechanism for the replacement of *Elymus* by *Ammophila,* the lack of a zone of decreased *Elymus* frequency at *Ammophila* patch borders suggests a more direct mechanism of species exclusion. Herbivory is an important factor in the microdistribution of *Cakile,* but microdistributions of other species are apparently influenced by other types of ecological interactions.

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ANNOUNCEMENT

"INTERFACE BETWEEN ECOLOGY AND LAND DEVELOPMENT IN CALIFORNIA"

This will be the title of a symposium to be held at the annual meeting of the Southern California Academy of Sciences, 1–2 May 1992 at Occidental College in Los Angeles. The meeting will begin Friday morning with a plenary address by Dr. Peter Raven, followed by morning and afternoon sessions on both Friday and Saturday. It is anticipated that the symposium will consist of four sessions on: Biodiversity and Habitat Loss, Mitigation of Development, restoration of Damaged Communities, and Wildlife Corridors. The focus of the meeting is to bring together persons involved in basic research, applied environmental consulting and governmental policy. For further information contact: Dr. Jon Keeley, Department of Biology, Occidental College, Los Angeles, CA 90041; 213-259-2958 (fax).